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Notes on the functional morphology of terminalia from *Prorates ballmeri* Nagatomi and Liu (Diptera: Scenopinidae: Proratinae) collected while in copula, with a description of the previously unknown female

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Abstract

A male and female specimen of *Prorates ballmeri* Nagatomi and Liu were collected while in copula. The specimens were dissected to find that the elongate distiphallus of the male had been inserted within the spermathecal ducts of the female. The association of the male and female genitalia for this species is figured and discussed in relation to associated taxa with similar genitalic features. The species was originally described from three male specimens, which did not allow for comprehensive study of the variation in many characters. The male is redescribed based on many newly collected specimens to include additional characters and the species variation and the previously unknown female is described. Additional notes on the taxonomy of the genus *Prorates* are included.

Key words: copulation, genitalia, mating, spermathecal sac

Introduction

The intermittent organ of male Scenopinidae (Diptera) is sclerotized and varies in structure and complexity among taxa. Some species possess extreme modifications in length and shape. One of these modifications includes the elongate tips of the bifurcate distiphallus, which in some species may be longer than the entire length of the fly. Beyond the descrip-

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tion of these structures, little is known about their function and how these elongated structures are manipulated during copulation. Kelsey (1976) reported the presence of a bifurcate, “coiled up, 30 mm long aedeagus” from a 4 mm long species of *Propebrevitrichia dionaeforma* Kelsey (Scenopininae) from South Africa, but noted that “a pair in copula shows no external evidence of this extremely long organ; where it goes and how it is manipulated is a mystery.”

Species in the genus *Prorates* Melander (Proratinae) possess many extreme modifications of the male genitalia such as the extended tips of the distiphallus and the elongate gonocoxal apodeme (Figs 1 and 2). The internal genitalic structure of female proratines, however, is mostly membranous and has been poorly studied because of the lack of associated female specimen.s of species described from only males and because of the difficulty in dissecting and visualizing these structures. Consequently, the interplay of the male and female genitalia during copulation is unknown for proratines as well as for all other scenopinids.

Recent collecting efforts in Utah by coauthor Irwin made available ethanol-preserved specimens of *Prorates ballmeri* Nagatomi and Liu in copula. This remarkable serendipity provides the first opportunity to describe the interlocking positions of the male and female genitalia of any scenopinid while in copulation. The male is redescribed to include additional characters and variation, the female is described, and the genitalia of the specimens in copula are figured and discussed.

Methods

Several male and female specimens were dissected to visualize their internal genitalia. Entire specimens or the abdomen dissected from specimens were bathed for 1 hour in saturated KOH at room temperature (approximately 25 ºC) to soften the cuticle. The specimens were then placed in 85% lactic acid and heated (approximately 70 ºC) until the nonsclerotized tissues were dissolved. The sclerotized tissues were then rinsed in 70% EtOH. Male terminalia were placed in glycerin for dissection and examination. Female abdomens were "folded open" by teasing the tergites and sternites apart along the pleural membranes. The entire female abdomen was then placed repeatedly in a bath of Chlorazol black stain (Chlorazol black powder dissolved in 70% EtOH) until the internal genitalic structures were visible. Partial teasing apart and manipulation of the soft tissue matrix surrounding the internal genitalic structures was often required to locate the stained spermathecae and spermathecal sac. When fully stained, the specimen was rinsed in 70% EtOH and/or placed in glycerin, where the unwanted portions of the tissue matrix were removed. General morphology follows McAlpine (1981) with additional terminology from Irwin and Lyneborg (1981a, b). Some structures of the male genitalia follow terminology from Nagatomi et al. (1994) and Winterton et al. (1999a). Terminology for structures of the female terminalia follows Irwin (1976) as modified by Winterton et al. (1999a, b),

Lyneborg (2001), and Metz et al. (in press). Each specimen was given a unique specimen code on an orange label in the format SCENOPINIDAE/M. E. Irwin/Specimen #/999999. These codes facilitate entry and manipulation of data into a systematic database within the architecture of MANDALA (Kampmeier et al. 1998) and are recorded as "MEI 999999" with their associated specimens throughout the text. All material examined is listed after the description. Museum codes used are as follows: BYU, Monte L. Bean Science Museum, Brigham Young University, Provo, Utah; CAS, California Academy of Sciences, San Francisco, California; EMUS, Entomological Museum of Utah State University, Logan, Utah; INHS, Illinois Natural History Survey Insect Collection, Champaign, Illinois; LACM, Los Angeles County Museum Insect Collection, Los Angeles, California; MEI, Personal Collection of Michael E. Irwin, Urbana, Illinois (ultimately to be deposited in CAS); UCR, University of California at Riverside Research Collection, Riverside, California; USNM, United States National Museum of Natural History, Washington, D.C.

Taxonomy of *Prorates*

Melander (1906) originally described *Prorates claripennis* as an empidid, but he later transferred this species to Bombyliidae: Heterotropinae (Melander 1928). The placement of this and subsequently described species of *Prorates* remained problematic with various authors (Efflatoun 1945, Melander 1950, Hull 1973) suggesting a possible closer affinity with species of scenopinids. Using a quantitative cladistic analysis based on morphology, Yeates (1992) hypothesized a monophyletic group including *Prorates frommeri* Hall, *Alloxytropus anomala* Bezzi, and *Caenotoides californica* Hall relative to other scenopinid taxa. He erected a separate subfamily within Scenopinidae, Proratinae, containing the species in these genera and supported a sister group relationship between *Prorates* and *Alloxytropus*. *Alloxytropus* was previously considered a synonym of *Prorates* by Melander (1928, 1950), Hall (1972), and Hull (1973).

The sister-group relationship of *Prorates* and *Alloxytropus* was supported by two synapomorphic character states: 1) the inner margin of the male eyes indented at the level of the antennal bases and, 2) the modified setae of tergite 2 composed of large, truncate setae with flattened or slightly rounded apices creating a triangular area at the posterior margin (Yeates 1992). Yeates (1992) also reported, however, that *Alloxytropus* possesses only a single antennal flagellomere, an apparent symplesiomorphy with the other scenopinids, while *Prorates* and *Caenotoides* possess two antennal flagellomeres. Nagatomi et al. (1994) deferred from making a single hypothesis of the relationships of the proratine genera, but acknowledged that *Prorates* and *Alloxytropus* were “closely related” and reported that *Prorates* could be distinguished from *Alloxytropus* by “having the cord-like phallus (just behind [the] hanging-bell phallus) forked anteriorly.” Nagatomi et al. (1994) also erected a new proratine genus, *Jackhallia* Nagatomi and Liu, determined to be “closely related to *Prorates* and *Alloxytropus*” from a single female specimen from Santa Cruz,

Argentina. They distinguished this genus based on the veins M_1 and M_2 arising independently from cell d instead of M_2 arising from M_1. Examination of this character among several specimens of *Prorates* suggests it is quite variable within a species. The validity of the species and their placement in these genera will require future phylogenetic investigation.

Prorates is represented by eight described species from the southwestern portion of the United States: *arctos* Hall, 1972, *ballmeri* Nagatomi and Liu, 1994, *boydi* Hall, 1972, *claripennis* Melander, 1906, *frommeri* Hall, 1972, *melanderi* Hall, 1972, *nigrescens* Hall, 1972, and *painteri* Nagatomi and Liu, 1994. A revision of the species of *Prorates* and their placement among the other proratine genera is the subject of ongoing study by coauthor Irwin.

The gonocoxal dorsal process (Fig. 2, GDP) (Nagatomi et al. 1994) and the amount of its posterior extension is herein considered an artifact and not a firm character among species. This is part of a sclerotized connection between tergite 9 and the gonocoxite, and the length of its projection varies depending on how it was dissected. Other characters among the species are diagnostic but are not included in the keys. The issue of species diagnosis will be addressed in the upcoming revision of the genus.

Prorates ballmeri **Nagatomi and Liu**
(Figs. 1-5)

Redescription and variation of males

Head. Dark brown; gray pruinose. Holoptic, eyes touching above frontal triangle. Inner eye margin curved around base of antenna, but not sharply indented; shiny black with an expanded portion of shiny black adjacent to antenna. Dorsal ommatidia larger than ventral with a clear horizontal line at level of antenna demarcating upper and lower ommatidia. Postocellar setae short, filiform, pale yellow. Gena narrow, pale yellow setose. Postgena pale yellow setose. Occiput lacking setae. Antenna dark brown, some specimens with pedicel light brown. Scape and pedicel gray pruinose; with a few fine, brown setae dorsally. Flagellomeres with short, fine, golden setae that are bent towards the apex. First flagellomere wider at base and slowly tapering towards apex. Second flagellomere cylindrical, slightly narrower apically. Style conical, terminal. Maxillary palpus one segmented; longer than antennae; cylindrical; yellow for basal 2/3 and brown on apical 1/3 – 1/2; with long, filiform, pale yellow setae. Mouth parts longer than head height; dark brown; sparsely yellow setose; labellar surface with few long, golden-brown setae.

Thorax. Dark brown, except postalar callous lighter; gray pruinose throughout. Scutum and scutellum with pale yellow, fine filiform setae. Scutum with sublateral and dorsocentral brown pruinose vittae. Scutal and scutellar macrosetae pale, golden-yellow

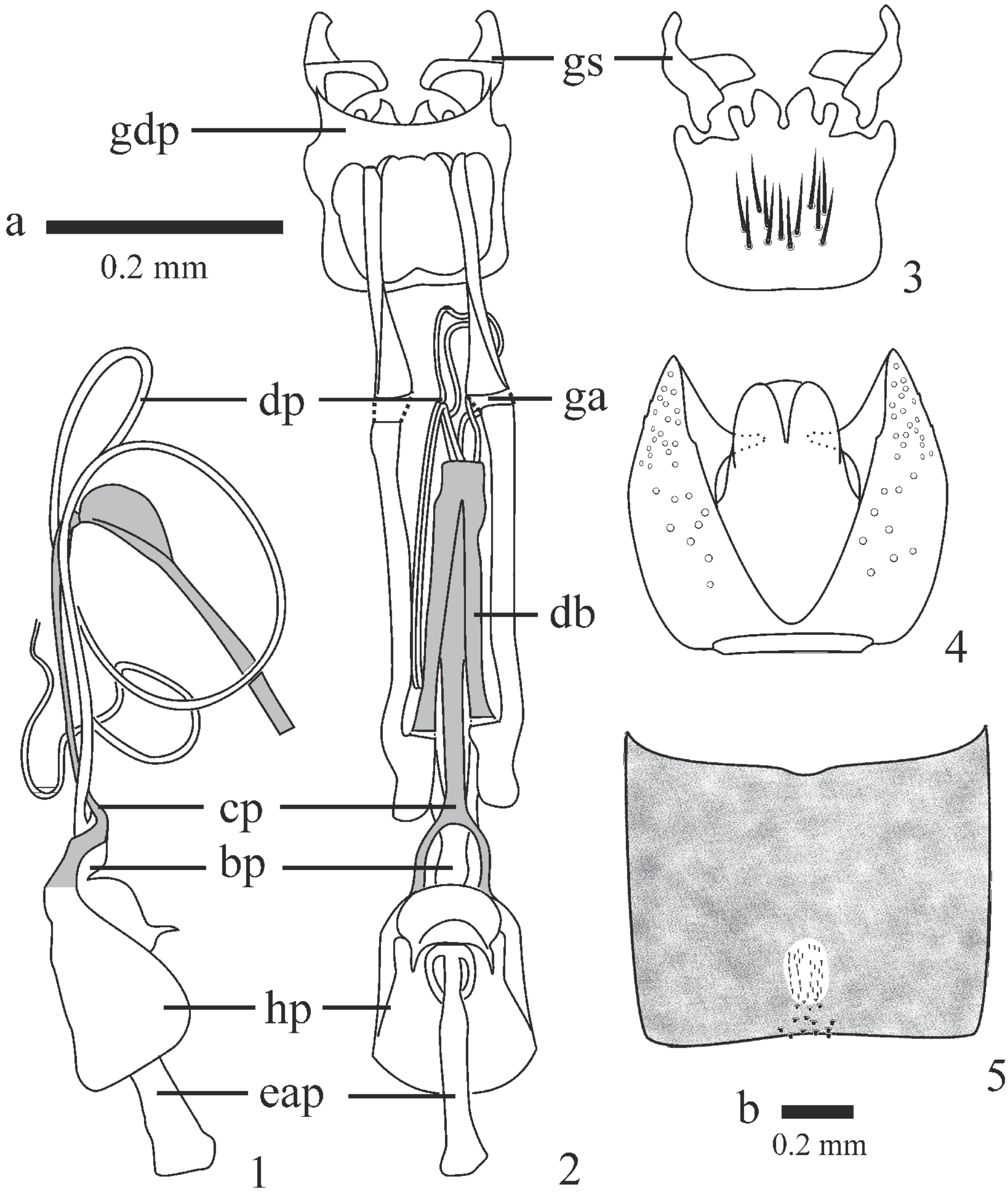
to light brown; sometimes pale at base and dark at apices. Notum with one or two notopleural, one postalar, and one scutellar pairs of macrosetae. Prosternum, proepisternum, proepimeron, posterior anepisternum, and ventral katepisternum short, filiform, pale golden setose; amount of setae varies considerable among specimens. Legs. Dark brown, apices of forecoxa and femora light brown to yellow; sparsely gray pruinose; short, filiform, pale golden setose. Fore- and midcoxae with long, filiform, pale golden setae anteriorly; hindcoxa with long, filiform, pale golden setae anterolaterally to posterolaterally; hind coxal knob extremely reduced, present as a low rounded point. Wing. Membrane hyaline, microtrichiose throughout; pterostigma pale brown; costa reaching R_5; vein M_2 arising from M_1 or separately from discal cell; veins M_1, M_2, and M_3 not reaching wing margin. Halter knob off white; base of stalk light brown.

Abdomen. Tergites and sternites dark brown, sparsely gray pruinose; sparsely short, fine filiform pale golden setose, with lateral setae and setae on basal segments longer. Modified setae on tergite 2 composed of an anterior pale, spiculate patch arranged in an ovoid pattern, longer than wide, and a posterior dark brown, broad, truncate patch arranged in a triangular pattern, spread out wider posteriorly (Fig. 5).

Terminalia. Tergite 8 only slightly modified, similar to previous segments; approximately half the length of tergite 7; anterior margin slightly acuminate medially, posterior margin emarginate medially; with one pair of sensory setae; dark brown; sparsely gray pruinose; sparsely short, fine filiform pale golden setose. Sternite 8 approximately half the length of sternite 7; quadrate, but wider posteriorly; brown; sparsely gray pruinose; sparsely short, fine filiform pale golden setose. Tergite 9 (Fig. 4); brown, light brown along margins; anterior connection between right and left halves dark brown; sparsely gray pruinose; sparsely short, fine filiform pale golden setose. Cerci (Fig. 4) bifurcate, subequal to extension of hypoproct; minutely setose apically. Hypoproct (Fig. 4) bluntly pointed posteriorly; minutely setose ventrally and apically. Subepandrial sclerite partially sclerotized. Gonocoxites (Fig. 2 & 3); brown; long, filiform, light brown setose ventromedially; gonocoxal ventral process projecting posteriorly and bifurcate apically. Gonocoxal apodeme (Fig. 2) brown, with an area just anterior to anterior gonocoxite margin dorsoventrally flattened and light brown, connection with dorsal bridge light brown. Gonostylus (Fig. 3) curved dorsomedially at apex; apex dorsoventrally flattened, scooplike; "cross-shaped" when viewed dorsally or ventrally; brown; glabrous. Dorsal bridge and cordlike phallus brown (Figs. 1 & 2). Hanging bell phallus (Figs. 1 & 2) short and broad; posterior ejaculatory bulb rounded with a dorsal, pointed extension; brown. Distiphallus (Fig. 2) light brown, bifurcate at base, distal coils longer than gonocoxal apodeme. Aedeagal apodeme (Figs. 1 & 2) robust, cylindrical; posterior end broadened laterally and ventrally creating a basket-shaped posterior face.

Description and variation of females

Generally lighter in color, but similar to males except as follows.



FIGURES 1-5. Male genitalia and tergite 2. 1, Lateral view of the male aedeagal apparatus showing only the left distiphallus tip, dorsal bridge and gonocoxal apodeme removed; 2, Dorsal view of gonocoxite and aedeagal apparatus; 3, Ventral view of gonocoxite; 4, Dorsal view of tergite 9, cerci, and hypoproct; 5, Dorsal view of tergite 2 with patch of modified setae. Cordlike phallus and dorsal bridge shown in gray to help clarify structures. Measure bar a is for all genitalia, measure bar b is for tergite 2 only. bp, basiphallus; cp, cordlike phallus; db, dorsal bridge; dp, distiphallus; eap, ejaculatory apodeme; ga, gonocoxal apodeme; gdp, gonocoxal dorsal process; gs, gonostylus; hp, hanging bell phallus.

Head. Dichoptic, frons at its narrowest width as wide as or wider than ocellar tubercle. Inner eye margin with shiny black edge less pronounced, but expanded portion of shiny black adjacent to antenna more pronounced. Ommatidia of uniform size. Scape and pedicel dark to light brown.

Thorax. Legs yellow to light brown.

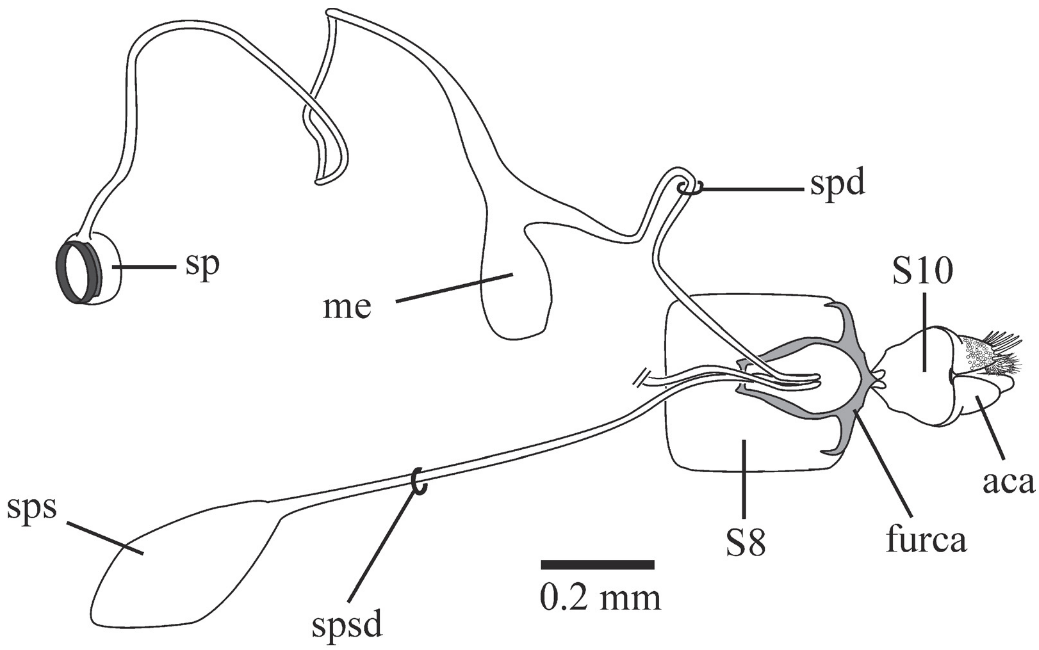


FIGURE 6. Female terminalia. aca, acanthophorite; me, membranous expansion of spermathecal duct; S8, sternite 8; S10, sternite 10; sp, spermatheca; spd, spermathecal duct; sps, spermathecal sac; spsd, spermathecal sac duct.

Terminalia (Fig. 6). Tergite 8 longer than wide; anterior margin straight; posterior margin with a narrow strip of cuticle connecting to tergite 9; dark brown; sparsely gray pruinose; sparsely short, fine filiform, pale golden setose. Membrane between tergite 8 and tergite 9 short, fine filiform, pale golden setose. Sternite 8 (Fig. 6) longer than wide; anterior margin straight; posterior lobe membranous, short, filiform, pale golden setose. Acanthophorites (Fig. 6) joined narrowly at dorsum and joined anterolaterally to sternite 10, with 5 pairs of robust, acuminate spines. Sternite 10 (Fig. 6) broader posteriorly; anterior margin with three anteriorly projecting points; ventrally brown; short, fine filiform, pale golden setose with a posterolateral to medial fringe of much longer setae. Cerci (Fig. 6) and hypoproct bulbous and membranous; minutely setose. Furca (Fig. 6) pear-shaped, narrower anteriorly; posterolateral corners expanded laterally into horn-shaped extensions that curve anteriorly. Spermathecal ducts and spermathecal sac duct (Fig. 6) arising from a common gonopore on the membrane of the furca. Spermathecal duct wider basally with a

membranous expansion (Fig. 6, me) at approximately half of its length then narrowing before terminating at the spermatheca; total length approximately ten furcal lengths. Spermatheca (Fig. 6) doughnut shaped with a sclerotized collar and neck on one side. Spermathecal sac duct subequal in width to the base of the spermathecal duct, slowly expanding towards sac; total length approximately four furcal lengths. Sac spherical, its length, width, and height subequal.

Distribution. Disjunct within the Great Basin Desert of the United States. It has been collected in Mono and Inyo Counties in California and Emery, Garfield, and Wayne Counties in Utah.

Ecology. Specimens have been taken by hand netting and are readily collected in numbers in Malaise traps. They are known to occur in dry washes and creek beds that range in habitats from *Artemisia* zones at 1375 m through the transition zone and into *Juniperus*/*Pinus* zones at 2100m.

Specimens Examined. USA, California, Mono County: 2 male paratypes (MEI 141895-6, UCR), S[c]herwin Summit, 6500 [ft], 24.V.1985, G.R. Ballmer. Inyo County: 2 males (MEI 141897-8), 6 females (MEI 141899-904) 17 mi E Big Pine, Death Valley Road, 6925 [ft], pinon-juniper zone, 21-24.VI.1992, Malaise, ME Irwin, DK Yeates. Utah, Emery County: 1 male (MEI 141842) and 1 female (MEI 141843) in copula, 2 km S Hatt's Ranch, 27 km SW Green River, Malaise in dry wash, 21-26.V.2002, ME Irwin, FD Parker, 1375 m, 38°50.5'N, 110°22.9'W; 1 female (MEI 141845), 2 males (MEI 141846-847), same data; 1 female (MEI 141844) same locality, 19-21.V.2002. Garfield County: 1 male (MEI 141848), Burr Trail, 45 km SE Boulder, Malaise in dry canyon wash, juniper woodlands, 23-27.V.2002, ME Irwin, FD Parker, 2190 m, 37°52.9'N, 111°06.7'W; 4 males (MEI 141905-8), 2 females (MEI 141909-10) Calf Crk., 10 km S Boulder, Malaise in side canyon, riparian vegetation, 23-25.V.2002, ME Irwin, FD Parker, 1750 m, 37°47.6'N, 111°24.9'W; 1 male (MEI 141853) same locality26-27.V.2002; 2 males (MEI 141863, 141866), 6 females (MEI 141850-51, 141877-80), Hall's Creek Overlook Road, nr main rd., Malaise in rugged rock wash, 23-27.V.2002, ME Irwin, FD Parker, 1670 m, 37°44.6'N, 110°55.2'W; 8 males (MEI 141854-61), 10 females (MEI 141849, 141881-9), Trachyte Ck at Hwy 276, Malaise on sandy bank, 22-27.V.2002, 1560 m, ME Irwin, FD Parker, 37°57.4'N, 110°34.3'W. Wayne County: 10 males (MEI 141852, 141862, 141864-5, 141867-72), 6 females (MEI 141873-8), Bull Mountain Road, 18 km S Hanksville, 22-27.V.2002. Malaise in dry wash, ME Irwin, FD Parker, 1620 m, 38°13.8'N, 110°40.6'W. Deposition of specimens is as follows: BYU (MEI 141905-10); EMUS (MEI 141854-5, 141862-3, 141877-8, 141882-3); INHS (MEI 141856-7, 141861, 141884-6); LACM (MEI 141866-8, 141879-81); UCR (MEI 141858-60, 141887-9); USNM (MEI 141852-3, 141864-5, 141869-71, 141874-6). The remaining specimens are deposited in MEI.

The description of the associated male and female genitalia (Fig. 7)

The terminalia are in opposite orientation to each other so that the ventral surface of the female's sternite 8 is facing ventrally while the ventral surface of the male's sternite 8 and gonocoxites are facing dorsally. The external terminalia are in close association, but the sclerites of the two sexes are not touching one another. Neither the male's gonostyli, which are articulated and musculated (Ovtshinnikova & Yeates 1998) and seemingly would serve a copulatory function, nor tergite 9, which has been suggested to possibly serve a clasping function in Asiloidea (Sinclair et al. 1994) is in contact with any female sclerites. The possibility exists that the specimens were once in closer proximity, but in death the genital sclerites retracted from one another.

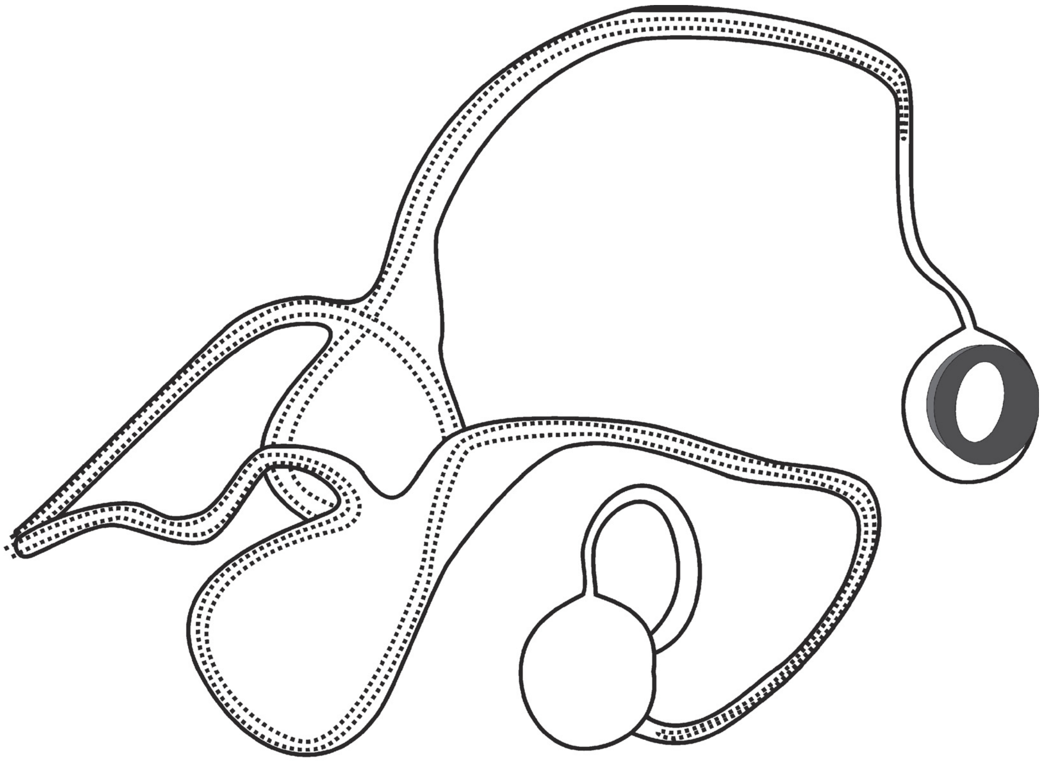


FIGURE 7. Female spermathecal ducts and spermathecae showing the insertion of the male distiphallus. The distiphallus is indicated by dashed lines.

The male's distiphallus is completely inserted into and partially uncoiled in the female's spermathecal duct (Fig. 7). Each of the separate bifurcations of the distiphallus enters into a different spermathecal duct, completes a full 360-degree turn in a membranous sac located approximately halfway along the spermathecal duct, then continues fur-

ther into the duct, finally reaching a point approximately 3/4 down the length of the spermathecal duct (Fig. 7). The tips of the distiphallus do not reach the spermathecae. The uncoiling of the distiphallus occurs entirely within the female abdominal cavity such that the basiphallus of the aedeagus is located at the entrance of the female gonopore (Fig. 7). The spermathecal sac is independent of any association with the male structures and "floats" freely within the abdominal cavity of the female.

Discussion

The opposite orientation of the terminalia suggest that either the male terminalia rotate on the longitudinal axis before or after copulation or that the male mounts the female dorsally and bends the tip of the abdomen ventrally and anteriorly in a "C" shape prior to copulation. The specimens were discovered "end to end," but still attached in the alcohol of a Malaise trap so no courtship or approach behavior was observed. The separation of the male's external sclerites, particularly the gonostyli, from the female was surprising. It is possible that these structures mechanically interact during courtship or during the early stages of copulation.

The observation of the remarkable route that the distiphallus travels down the spermathecal duct lends itself to a conjectural discussion. No muscles that originate from within the male terminalia themselves attach to these structures (Ovtshinnikova & Yeates 1998). Likewise, there does not seem to be any correlated structures on the female that would induce the distiphallus to enter the spermathecal ducts. How these fragile, sclerotized structures uncoil and enter the spermathecal ducts remains a mystery and the act itself seems to defy any physical explanation we contrive. Pneumatic or hydraulic mechanisms could possibly explain this phenomenon and might be explored using fluid models, but these are beyond the scope of this paper.

This research contains the only formal description of the presence of a spermathecal sac in Scenopinidae. The spermathecal sac was previously described only from species in the family Therevidae (Winterton et al. 1999b) and Mydidae (Irwin & Wiegmann 2001), however, we have located a similar structure in species from several asiloid families (Asilidae, Apioceridae, Apsilocephalidae, and Scenopinidae) and our current hypothesis is that these structures are homologous. The function of the spermathecal sac is unknown, but on some species of therevids has a volume occupying as much as 70% of the abdominal cavity (Winterton et al. 1999b), which would imply an important role in the female's biology. Winterton et al. (1999b) postulated that the spermathecal sac in Australian therevids serves as a reservoir for male accessory gland secretion and/or as a preliminary reservoir for sperm prior to its transfer to the spermathecae. Our current observation of the extremities of the distiphallus of *P. ballmeri* males inserted deep within the spermathecal ducts makes it difficult for them to inject anything into the spermathecal sac. The current observation suggests that the sac may form a reservoir for secretions of female origin in the species of

Prorates, as all species have very elongate distiphallus tips and are assumed to function in a way similar to *P. ballmeri*.

As with many scientific observations, this research causes the development of more questions than it has answered. It is rare to have the opportunity to study the interaction of male and female genitalia among Insecta when the vast inventory of study material is dry and pinned. However rare, the amazing correlation of these structures should be investigated further as this and future discoveries lend themselves to exploring new avenues of functional morphology and character evolution.

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